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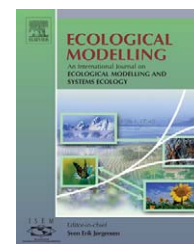**ScienceDirect**

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Habitone analysis of quaking aspen in the Utah Book Cliffs: Effects of site water demand and conifer cover

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ABSTRACT

Quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America, but its presence is declining across much of the Western United States. Aspen decline is complex, but results largely from two factors widely divergent in temporal scale: (1) Holocene climatic drying of the region has led to water limitation of aspen seedling recruitment, and (2) anthropogenic fire suppression during the 20th century has allowed shading of aspen clones by fire-intolerant conifers. These processes interact variously and often diffusely, but traditional, binary habitat mapping approaches can only resolve their net effect after complete loss of aspen patches. To provide information for preemptive land management in the Book Cliffs – a biogeographic link between the Utah and Colorado Rocky Mountains and a location experiencing aspen decline typical of the region – we developed a regression-based generalization of niche/habitat analyses that is usable in GIS, is capable of detecting anomalies in cover before complete patch conversion, and can be incorporated smoothly into the decision-making process. We estimated the realized Hutchinsonian niche of quaking aspen to potential evapotranspiration (PET) by nonparametric, likelihood-based regression techniques, projected (continuous) values of aspen's niche expectation and uncertainty geographically, and correlated differences between observed and expected aspen cover to remotely sensed conifer cover. Results confirm the strong constraint of site water demand on aspen cover and suggest that conifer cover decreases aspen cover beneath its expectation given the PET environment. Compared to sites without quaking aspen, our aspen sites have lower PET in every month of the growing season, but the difference increases over the growing season as drought effects become more extreme. Superimposed on this broader environmental constraint, conifer cover displaces aspen cover and shows a positive correlation with model deviance ($r = 0.344$). Ultimately, the thematic information conserved by our approach allowed us to resolve detailed rasters of management potential and map a modest potential increase of aspen cover – 14.63 ha (0.14%) of the study area, or +2.46% of current aspen cover – within one management cycle.

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1. Introduction

With a range extending from the Arctic Circle to the tropics, quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed native tree species in North America (Little, 1971). However, aspen coverage in the Intermountain region of the Western United States is in apparent decline (Table 1) due to factors acting at disparate spatial and temporal scales. Aspen decline is most often attributed to Holocene climate change (Baker, 1925; Cottam, 1954; Maini, 1968) and succession to conifers following 20th century fire suppression (Baker, 1925, 1949; Meineke, 1929; Jones, 1967; Loope, 1971; Schier, 1975; Mueggler, 1976; Jones and DeByle, 1985), but also to overgrazing by wild and domestic ungulates (Gruell, 1970; Krebill, 1972; DeByle, 1985; Kay, 1993, 1997, 2001a, 2001b, 2001c, 2001d; Hart and Hart, 2001a, 2001b; Rolf, 2001a, 2001b) and disease (Gruell, 1970; Krebill, 1972; Hart and Hart, 2001a, 2001b). Of special interest to local human populations, substantial hydrological (Gifford et al., 1984), aesthetic and recreational (Johnson et al., 1985), and biodiversity (Kay, 1997) amenities will likely be forfeited with further losses of the region's aspen cover.

Quaking aspen's climatic environment appears to be the broadest constraint on its geographic distribution. Its seeds are short-lived, and its seedlings have a narrow tolerance with respect to temperature and moisture (Maini, 1968). In the Intermountain West, soil moisture conditions favoring germination and recruitment occur extremely rarely, and so disturbance-triggered asexual reproduction, or "suckering," is credited with maintaining extant quaking aspen coverage (Baker, 1966). In many locations, chronic disturbances such as fire, wind-throw, disease, and insect outbreak result in the persistence of large, spatially discrete aspen patches. These patches are composed of one or more clones, each ranging from a few square meters to nearly 200 ha (Baker, 1976).

Quaking aspen is shade-intolerant (Baker, 1949), and adult stem mortality has been attributed to shading by conifers (Loope, 1971; Schier, 1975). In the absence of canopy disturbance sufficient to remove competitors and trigger suckering, sites require from 70 to 200 years (Baker, 1925; Meineke, 1929; Jones, 1967) to convert from aspen- to conifer-dominated communities (Mueggler, 1976). Thus, by removing wildfire's constraint on coniferous tree establishment and its triggering effect on aspen's asexual reproduction, 20th century fire suppression programs appear to have exacerbated aspen decadence and type-conversion (Jones and DeByle, 1985).

Realizing the importance of aspen decline to hydrologic, biological, aesthetic, and other land values, land managers seek means of assessing and rehabilitating aspen over large areas in the Intermountain West. These goals require flexible, informative means of assessing aspen's cover and potential over large areas, while retaining as much information as possible on aspen cover at individual sites. To this end, we report an analysis of quaking aspen's relationship to site water demand and conifer encroachment in the Book Cliffs of Utah (Fig. 1), an area that is both biogeographically important to aspen's range and ideally suited for studying the relationship between climatic and successional constraints. These constraints operate at vastly different spatial and temporal scales, and their interaction should be most apparent on the receding edges of aspen's biogeographic range (Brown, 1995).

We studied the effects of these constraints on aspen in the Book Cliffs hierarchically, in a regression-based habitat framework, which we refer to as habitone analysis. Although we were at first reluctant to beleaguer ecologists with yet another term, we found the term "habitone" an intuitive contraction between "habitat" and "ecotone" and expedient in comparison to repeated explanation of its divergence from binary, classification-based habitat analyses. Habitone analysis draws from conventional niche/habitat ordination and classification techniques, but is regression-based and supports ecological interpretation of model validation, and so is therefore a novel enhancement to be distinguished from these approaches.

2. Methods

2.1. Study area

The 10,450-ha study area is located in the Book Cliffs near the Utah-Colorado (U.S.A.) border (Fig. 1), on the steeply dissected, north-facing slope of the southern crest of the Tavaputs Plateau. In the Ecoregion framework (Bailey, 1998; McNab and Avers, 1994), the 2000- to 3000-m-elevation Tavaputs Plateau is an approximately 230-km latitudinal band that descends gently into the semiarid Uinta Basin to the north and drops abruptly into the arid Northern Canyonlands of the Colorado Plateau to the south. Bounded longitudinally by these comparatively arid regions, the Tavaputs Plateau forms the most

Table 1 – Current and historical (i.e., prior to European settlement) aspen cover in the Interior West (from Bartos and Campbell, 1998a)				
State	Current aspen (ha)	Historical aspen (ha)	Decline (ha)	Decline (%)
Colorado	444306	875201	430896	49
Utah	571189	1172274	601084	51
New Mexico	56091	456671	400580	88
Wyoming	81586	174584	92998	53
Arizona	11604	288352	276748	96
Idaho	248608	643819	395175	61
Montana	84418	236270	151851	64
Nevada	47507	No data	–	–
Total	1545309	3847170	2349332	60

Fig. 1 – The biogeographic context of the study area. The study area is located on the most contiguous biogeographic link between the Utah and Colorado Rocky Mountains. Broadly estimated aspen habitat (NRCS Plants Database) is highlighted in purple.

contiguous biogeographic link between the higher sub-alpine communities of Utah's Overthrust Mountains and Colorado's North-Central Highlands of the Rocky Mountains. Under current climate conditions, the Book Cliffs and the study area within them constitute a residence and potential corridor for the long-term movement of flora and fauna between larger, continuous expanses of sub-alpine climates and associated biotic communities.

Monthly mean temperatures averaged across the Tavaputs Plateau range from −5 to 20° C, and the Plateau's average annual temperature is approximately 7° C (Daly et al., 1994). Plateau-average monthly precipitation totals range from 28 to 39 mm, and its total annual precipitation average is approximately 408 mm. Temperatures are strongly seasonal, and precipitation shows weakly bimodal seasonality (Daly et al., 1994).

Initially suggesting the hypothesis of climatic constraint, the landforms of the study area serve as intuitive, visual proxies for underlying environmental gradients. Within the broadly north-sloping extent of the study area, quaking aspen is located primarily on minor north-, northeast-, and northwest-facing slopes. More rarely, where ridges terminate into canyon bottoms within the study area, small patches of quaking aspen often appear at points where low-order canyons converge, and "stringers" of quaking aspen also occupy the bottoms of slight, presumably moister, crenulations in otherwise smooth east- and west-facing slopes. The northern boundary of the study area truncates a longitudinal and elevational trend of increasing conifer cover. The most prevalent conifer, Douglas-fir (*Pseudotsuga menziesii* Mirb.) is scattered across all landforms except the broader, sagebrush-dominated canyon bottoms, and increasingly dominates all but these shrub-dominated lands as the Tavaputs Plateau dips gently to the north. In the absence of fire, successional dynamics of aspen and other vegetation communities in the study area appear to stabilize in Douglas-fir dominance—although on toe slopes, aspen communities appear to convert to sagebrush-dominated communities typical of more xeric sites.

2.2. Data

2.2.1. Landcover

Steep topography and low vegetation stature on ridges permitted complete census of the study area from ridgeline transects (Fig. 2). Standing on these transects, a pair of observers surveyed each patch of quaking aspen in the study area, drawing patch-bounding polygons onto USGS 7.5-min topographic quadrangles during the summers of 2001 and 2002 (Fig. 2). These maps were digitized and rasterized to 30-m resolution, assigning to each raster cell the fraction of it covered by aspen patches: complete aspen cover in patch-interior cells, the fraction of patch coverage in cells intersecting a patch edge, and the sum of patch coverages in cells containing the edges of two patches. Thus, the resulting raster of aspen cover held a fraction of aspen cover in each cell: 1.0 cover for interior cells, less than 1.0 cover for edge and multi-edge cells, and 0.0 for non-aspen cells.

The aspen-cover raster was refined to incorporate Douglas-fir canopy cover. This cover was estimated allometrically from diameter-at-breast-height and canopy-height measurements taken during the summer of 2001 in 139 plots in two randomly selected canyons within the study area (Fig. 2). The plots in each canyon were spaced approximately 200 m apart along elevation contours and randomly between 100 and 200 m apart across elevation contours. Over-, mid-, and under-story cover of Douglas-fir within each plot was estimated from the field measurements through the allometric equations of the Central Rockies variant of the U.S.F.S. Forest Vegetation Simulator (Johnson, 1997a, 1997b; Dixon, 2001; Sexton, 2003) and summed to a single value for each plot.

These Douglas-fir percent-cover data were used to train a Generalized Linear Model (GLM, Poisson distribution) (Hastie
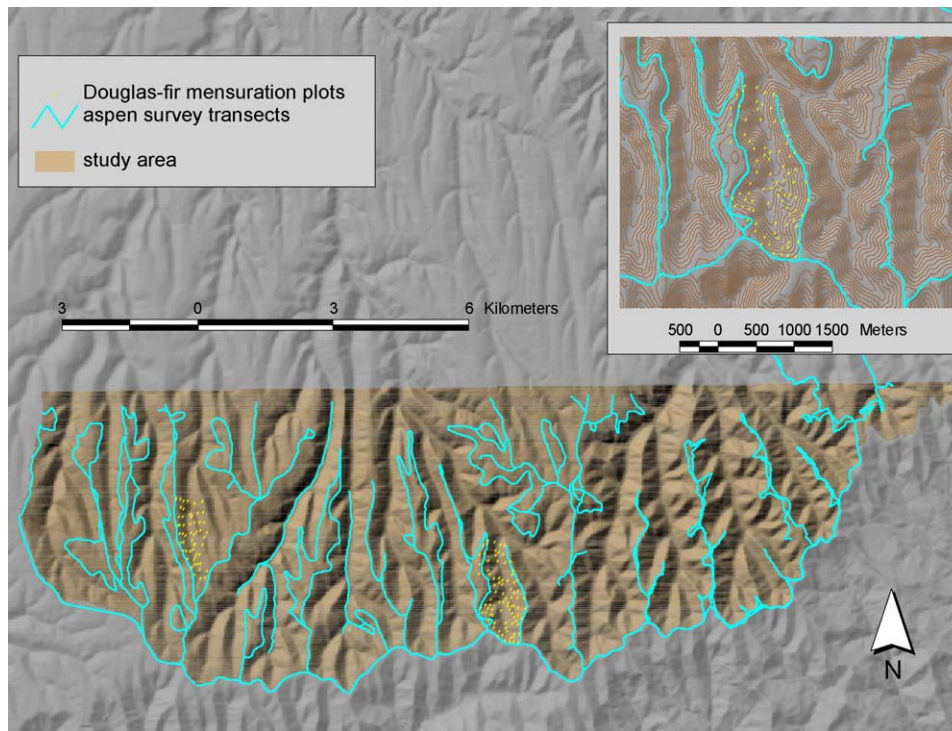
Fig. 2 – Spatial sampling/survey design for field-measurement of aspen and Douglas-fir cover. Outlines of aspen stands were surveyed from transects located along ridgetops and roads, and Douglas-fir DBH was measured in 139 plots placed within 2 randomly selected canyons of the study area. The inset details the spatial distribution of Douglas-fir mensuration plots within the more eastern of the two randomly selected canyons. To show topography, both the main map and the inset were hillshaded with a solar azimuth of 315° and altitude of 45°.

and Pregibon, 1992; Guisan et al., 2002) relating Douglas-fir canopy cover to rasters calculated from georectified, terrain-corrected, spring and fall Landsat 7 Enhanced Thematic Mapper Plus (ETM+) images, USGS 30-meter digital elevation models (DEMs), and the field-surveyed 30-m quaking aspen raster.

Fall and spring Normalized Difference Vegetation Index (NDVI) (Deering et al., 1975):

$$NDVI = \frac{B4 - B3}{B4 + B3}, \tag{1}$$

where B3 and B4 are ETM+ bands three (i.e., "red" [0.630: 0.690] μm) and four (i.e., "near infrared" [0.750:0.900] μm), were used for their positive correlation to persistent-leaved vegetation canopy cover. ETM+ bands 1, 2, and 3 correspond respectively to the blue ([0.450:0.515] μm), green ([0.525:0.605] μm), and red ([0.630:0.690] μm) absorption spectra of photosynthesizing vegetation (Jensen, 1996), so a sum of fall brightness values of these bands was chosen to further discriminate bare soil from vegetation. A sum of modeled potential shortwave radiation for the months of November and April (Zimmermann, 2000a) was included to integrate the ancillary effects of topography and low sun-angle of fall and spring on the remotely sensed variables. Quaking aspen cover was included to limit over-prediction of Douglas-fir in quaking aspen stands due to the similarity of shade from aspen and Douglas-fir crowns.

The sign of each regression coefficient was intuitive, and every coefficient was highly statistically significant, with standard error on each equaling less than one-fifth the estimated value (Table 2). The model accounts for approximately 68% of the null deviance in the data ($D^2 = 1 - d_r/d_{null} = 0.679$), and is parsimonious with degrees of freedom ($D^2_{adj} = 0.668$). Mean absolute error (MAE) is ±2.72% cover, but the presence of a few strong outliers is suggested by the large standard deviation of the MAE (S.D.$_{MAE}$ = 5.753) and high MSE (MSE = 40.267) relative to the MAE.

The modeled Douglas-fir percent cover was then adjusted for random crown overlap (Crookston and Stage, 1999) and divided by 100 to create a raster of Douglas-fir fractional cover. Finally, the fuzzy landcover partition (Wang, 1990) was com-

Table 2 – Summary of Douglas-fir percent cover regression			
Variable	Coefficient	S.E.	$p(\chi^2)$
(Intercept)	10.053	0.468	<0.001
AspenPatch	−1.487	0.131	<0.001
fall.b123	−0.051	0.006	<0.001
fall.ndvi	10.769	1.386	<0.001
spr.ndvi	4.986	0.909	0.001
sf.shrtwv	−7.6E−5	1.2E−5	<0.001

pleted by adding a nonforest class to the landcover dataset as an "out" class, and its values were calculated simply as the difference between 1.0 and the sum of aspen and Douglas-fir cover.

2.2.2. Potential evapotranspiration

Rasters of monthly potential evapotranspiration, in units of 1 mm/day, were calculated using software (Zimmermann, 2000b) that applies an empirical equation calibrated for the arid Western U.S. (Jensen and Haise, 1963) to a set of monthly mean (1971–2000) daily air temperature rasters, in units of °C (Daly et al., 1994) and monthly mean (1971–2000) daily total solar radiation rasters, in units of kJ/m^2/day, as the sum of monthly shortwave and diffuse radiation (Zimmermann, 2000a, 2000c). Estimates of PET equaled zero for months in which the mean temperature was less than or equal to zero, and so only the growing-season months of March–October were included in the analyses.

2.3. Habitone analysis

2.3.1. Estimates of aspen cover expectation and deviance

Habitone analysis is conceptually identical to traditional, niche-based habitat analyses, except that it accommodates continuous measurements of presence (i.e., cover), and generalizes interpretations to do so. In this analysis, we drew upon a raster implementation of fuzzy set theory (Zadeh, 1965; Wang, 1990) and likelihood-based statistics to interpret and estimate the continuous-scale habitat maps. The general procedure is simpler than traditional methods of habitat mapping because the thresholding step that converts continuous estimates to binary representation is omitted, resulting in more informative maps due to the increased variability retained (Wang, 1990). Interpretation of cover-expectations is consistent with the Hutchinsonian niche (Hutchinson, 1957) and gradient analysis (Whittaker, 1956), and deviations from expectations are interpreted through likelihood-based indices. The framework is not specific to any dimensionality of the environment, and so ordination is a useful but not absolutely necessary step for viewing the distribution of cover in the environment. In this application, the environment (PET) was simple enough to be viewed on a temporal axis without statistical ordination.

To project aspen's niche in an environmental domain of monthly PET, eight aspen–PET response curves – each associated with 1 month of the growing season – were estimated in a generalized additive modeling (GAM) approach (Hastie and Tibshirani, 1990; Austin, 2002; Guisan et al., 2002) using the Friedman Super-smoother with four target degrees of freedom and then graphed over a time-series of PET axes. A GAM approach was used because it is a flexible nonparametric extension of general linear models, capable of simplifying aspen's empirical distribution in the PET environment with few parametric assumptions, although any sufficiently flexible regression technique could have been used (see Moisen and Frescino (2002) for a comparison of algorithms). The determinacy of each relationship, as measured by its model's overall $D^2 = 1$ – residual/null deviance, was plotted over the respective growing-season months to describe temporal variability in the response.

To map aspen habitone with respect to PET, mapped aspen cover was regressed on a sample of cells using a regression tree (CART; Breiman et al., 1984; Džeroski and Drumm, 2003), chosen because regression trees assume no distribution *a priori*, are insensitive to linear transformations of the data, algorithmically perform variable selection, and produce models that can be easily encoded in a GIS. A statistical module extension (STATMOD; Garrard, 2003) for ArcView 3.2 (ESRI, 2002) was used to impute the habitone maps on the PET rasters from a text file of the fitted tree model.

A random sample of 10% of the landscape was initially selected for regressing aspen's response curve over PET. At each selected observation, values of PET for each month of the growing-season (i.e., March–October) were stored with the fuzzy cover of aspen in that cell. Cells with missing values on any dimension were removed (mostly due to study-area edges), yielding a final training sample of 9.93% of the ($N = 116,116$) population. An initial regression tree was calibrated with 128 terminal nodes and a mean residual deviance of 0.030, cross-validated, and pruned to 40 terminal nodes. Aspen's habitone expectation, i.e., the predicted fractional aspen cover of each terminal node, and habitone deviance, calculated by dividing each terminal node's deviance by its (sub-)sample size, were then estimated across the landscape by applying the final tree to the PET vector at each cell. Expected aspen cover was subtracted from the observed aspen cover raster, providing a map of over- and under-occupied locations, or positive and negative aspen anomaly, respectively.

2.3.2. Fuzzy-logical estimation of management potential

As well as aspen cover, aspen management is constrained by aspen's relationship to its environment. To sustain the amenities provided by aspen, the current management objective in the Book Cliffs is to increase aspen cover in suitable locations. However, it is economically and biologically infeasible to augment aspen cover via seeds or seedlings, and impossible to expand aspen via suckering where aspen are not currently in close proximity. Management is therefore constrained to manipulate the environment at locations adjacent to existing aspen so as to initiate clonal expansion. These rules are encoded through fuzzy logic (Zadeh, 1965; Roberts, 1986; Silvert, 2000) in the equation:

$$\hat{\delta}(x_{i,j}) = \mu'_{\text{aspen}}(x_{i,j}) \cap \hat{\mu}_{\text{aspen}}(x_{i,j}) \cap \sum \frac{\mu_{\text{aspen}}(x_{i\pm1,j\pm1})}{8}, \quad (2)$$

where management potential $\hat{\delta}(x)$ is calculated for each cell $x_{i,j}$ using the logical intersection of aspen absence at $x_{i,j}$, $\mu'_{\text{aspen}}(x_{i,j})$, aspen's expectation at x, $\hat{\mu}_{\text{aspen}}(x_{i,j})$, and the mean aspen cover at x's eight immediate neighbors, $\sum \mu_{\text{aspen}}(x_{i\pm1,j\pm1})$. Due to the continuous scale of all the variables involved, fuzzy logic was used instead of classical, Boolean logic. The fuzzy intersection operator, $\cap$, is a generalization of the Boolean intersection, "AND", and calculates the minimum of its arguments. The equation therefore translates to "the minimum of aspen absence and aspen expectation at a cell and aspen cover at its eight nearest neighbors," or again, "*the degree to which* aspen covers the cell, AND aspen is expected in the cell, AND aspen covers the cell's neighborhood".
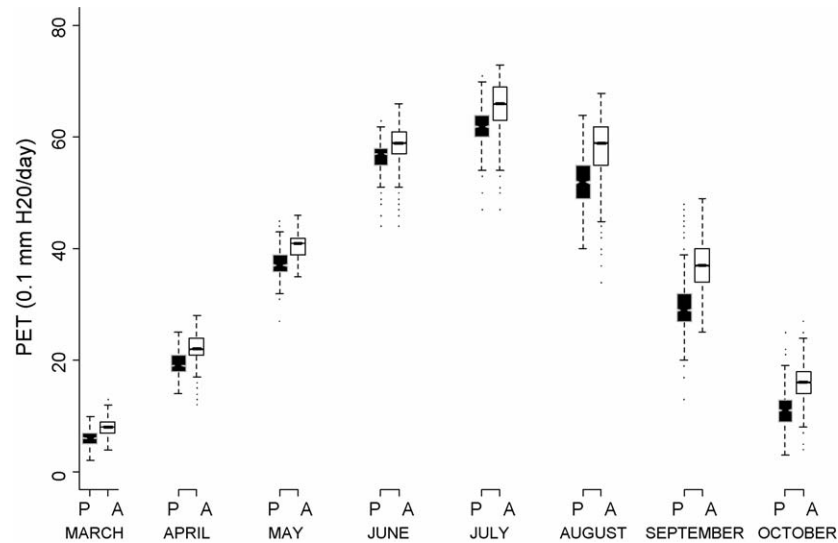
Fig. 3 – Distribution of PET values (0.1 mm H_2O/day) for aspen-present "P" and aspen-absent "A" samples (with $\mu_{aspen}(x) > 0.0$ classified as "present") over growing season months (n = 11,583). The boxes represent the range between the second and third quartiles of the data, medians are displayed as notches through the boxes, the 95% confidence intervals by pairs of staples, and outliers by points.

3. Results

Potential evapotranspiration in aspen-present ($\mu_{aspen}(x) > 0.0$) and aspen-absent ($\mu_{aspen}(x) = 0.0$) samples both tracked the overall seasonal PET pattern (Fig. 3), with the aspen sample having lower PET than the non-aspen sample in each month of the growing season. The difference in PET between aspen-present and aspen-absent samples was small and relatively constant in the early and middle growing season, but increased in the late growing season, from August to October. The largest PET difference between aspen and non-aspen samples appeared in September.

Aspen cover in each spatial cell over the study's time period was taken as constant, but aspen's statistical expectation over monthly PET varied among the growing-season months. Clearly, this is not to be interpreted as aspen mobil-

ity on such short time scales, but instead should be seen as seasonally fluctuating climatic constraints on a relatively constant aspen distribution. Aspen's response to PET in April–July decreased monotonically with increasing PET, but in March, August, September, and October, each monthly response curve was modal, decreasing nearly symmetrically about a single maximum at intermediate PET values (Fig. 4A). (N.B. GAMs tend to skew the values at the edges of a variable's range toward the values in the interior, so each of the curves has a slight upward shift at the low-PET end of the range.) The maximum expected aspen cover over each PET month – or niche optimum – was lower in the summer than at the vernal and autumnal edges of the growing season and higher in the late- as opposed to early growing season. The determinacy (D^2) of aspen's PET niche varied smoothly between maxima of approximately 0.35 at the edges of the growing season to a June minimum of about 0.13 (Fig. 4B).
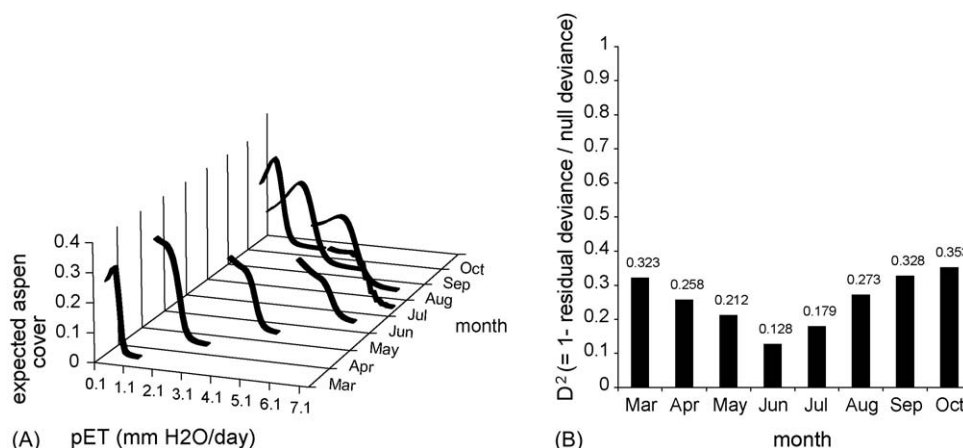
Fig. 4 – Aspen's expectation over PET (A) and related deviance (B) over growing season months.
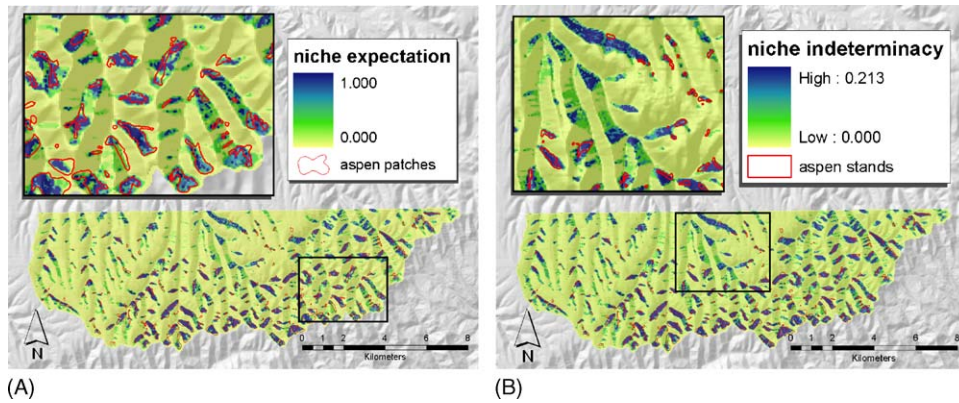
Fig. 5 – Maps of aspen's expectation (A) and indeterminacy (B) as a function of potential evapotranspiration. Hillshading in main images is as in Fig. 2; topography in insets is exaggerated 5× to accentuate landform relationships.
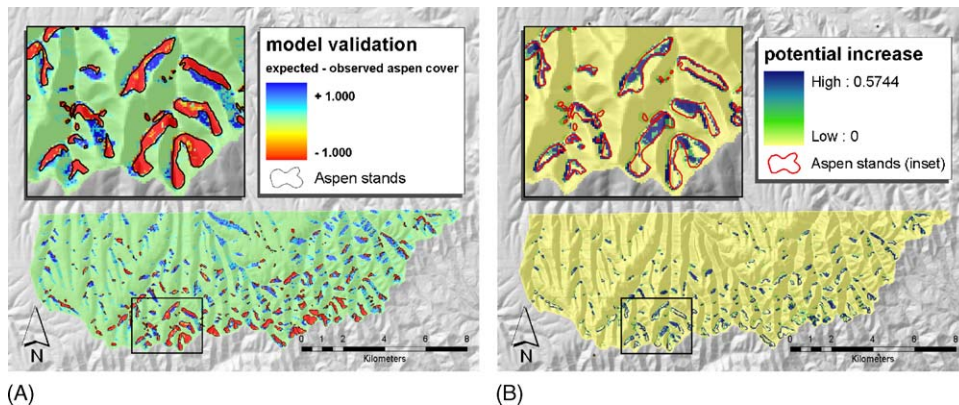
Fig. 6 – Maps of expected-observed aspen habitone validation (A) and management potential (B). Main images and insets are hillshaded as in Fig. 5.

The pruned regression tree consisted of 40 terminal nodes with mean residual deviance of 0.033 (Sexton, 2003). The $n = 11,530$-cell training sample of the population was large and random, and the regression tree imposed no *a priori* distribution on the data. The model of the empirical aspen–PET relationship may be assumed unbiased and steady-state, and the tree simply redistributed the *observed* aspen cover across the landscape as *expected* aspen cover according to position in PET-space (Fig. 5A) with no change in overall cover (Guisan and Zimmermann, 2000). Thus, the total expected cover equaled the total measured cover, $\hat{\mu}_{aspen}(X) = \mu_{aspen}(X) = 0.057\ X = 595.68/10\ 450.44$ ha. However, the large count of zero-aspen cells appeared to pull the distribution of expected values toward low, but non-zero, values. The mean indeterminacy of the model aspen–PET relationship $d_r(X)$, was 0.033, with a large proportion of zero-values and no values estimated above 0.25 (Fig. 4), consistent with the GAM results. Aspen–PET indeterminacy was positively correlated with measured aspen cover ($r = 0.514$) and expected aspen cover ($r = 0.940$).

Geographically, unoccupied aspen habitat (i.e., locations with aspen expectation greater than zero and observation equal to zero) covered 4.8% of the study area, but was more prevalent in western and northern portions of the area (Fig. 6).

Nearly all cells of positive aspen cover were in excess of their expectation. Although only 2.0% of the area was occupied jointly by expected aspen and actual Douglas-fir cover, their correlation coefficient (r) was 0.344. This correlation coefficient of measured and expected aspen cover was 0.459, and was 0.383 between aspen–PET indeterminacy and Douglas-fir cover. These niche values, when projected onto the landscape along with the management constraints in Eq. (1), shows a potential increase in aspen cover at 289 cells (Fig. 6B), which, when multiplied by the positive management potential of each cell, equal 0.14%, or 14.63 ha of the study area.

4. Discussion

4.1. Aspen's PET niche

Quaking aspen cover in the Book Cliffs appears to be constrained primarily by site water balance over the growing season, although the strength of this constraint varies across months. Each of the response curves represents the aspen cover expected over the range of PET in that month, and this expectation changes monthly due to the fluctuating spatial distribution of PET in relation to seasonally constant aspen

cover. Although unintuitive at first, the monthly resolution of aspen's PET niche yield insights into its environmental constraints. At the low end of the PET range, especially at the autumnal end of the growing season, aspen appears to be strongly constrained by low energy. The most plausible explanation, given quaking aspen's shade intolerance, is low incidence of photosynthetically active radiation, such that these locations in general cannot support aspen's metabolism and therefore support less aspen cover than sites where this need is met more fully. This relationship also appears in March, but in April, May, June, and July, when sunlight is less likely to be limiting, aspen finds weaker constraint on the low end of the PET gradient. Aspen's expected cover is not fully constrained to zero by low PET values of any month, however. Although low solar energy availability constrains aspen cover to some degree, sufficient constraint of aspen by low sunlight is never reached within the extent of this study.

Aspen's response to PET declines to zero in cells that have a high PET value for every month, suggesting that low water availability is a stronger constraint than low energy availability in the study area. However, as PET incorporates information most directly on energy availability and only very indirectly on water availability, this conclusion remains conjectural. Given the modal, nearly symmetric (albeit truncated) response curves of aspen in the early spring and later half of the growing season, the study area's aspen cover seems to be balanced between energy and water shortages at those times, and the addition of a water-supply dimension in each month would provide a more informative set of axes upon which to project aspen's niche (Stephenson, 1990).

The determinacy of aspen's PET niche, although low for any single month, shows that nearly all of the variation in aspen cover over the study area is explainable by aspen's relationship to PET over the growing season. However, the relationship's indeterminacy increases with both measured and expected aspen cover, so dense or pure aspen are unlikely scenarios given this relationship, and aspen presence is much less determined by PET than is aspen absence. Comparatively, Douglas-fir cover appears to be strongly positively associated with aspen–PET indeterminacy, and is therefore likely a strong factor in aspen's under-occupation of cells.

4.2. Management implications

Interpretable as aspen's under- and over-occupation of cells, the habitone validation map (Fig. 6B) can be considered a spatially explicit, ecological hypothesis of the ability of external environmental factors (i.e., management action) to change current aspen cover. Whereas the majority of the Book Cliffs appear to be fully constrained to zero aspen cover by water demand (Fig. 5), large contiguous patches exist where measured aspen cover is either above or below its expectation. Further, aspen–PET determinacy is negatively correlated with measured aspen cover, meaning that extant aspen cover is less assured by the PET environment at higher aspen coverages. However, determinacy is also negatively correlated with expected aspen cover, and areas exist where aspen is absent, habitat exists, and determinacy is low. Therefore, areas exist where management could increase aspen cover.

Given the management scenario modeled, aspen increases will be located mostly on the periphery of current aspen patches (Fig. 6), as is consistent with aspen's clonal expansion. We estimate a potential increase in aspen cover of 0.14%, or 14.63 ha of the study area—a 2.46% increase from current aspen cover in one management iteration. Locations where management might increase aspen concentration in the Book Cliffs are scattered diffusely in space, and so management will need to attain economies of scale, possibly through a combination of prescribed and wild fire and by reduction of use by wild and domestic ungulates.

4.3. Landscape dynamics of the Book Cliffs

The Book Cliffs are a spatially discrete edge of aspen's biogeographic range, and it is on such a sharp ecotone that one would expect the most rapid changes in aspen's cover over time (Brown, 1995). It appears that at least two of the recognized factors – climate change and conifer invasion – are acting to reduce aspen's occupation of the study area, but with differing patterns in space and time. However, the two factors do appear to be interrelated. The northward trend of increasing aspen-habitat occupation by Douglas-fir suggests an upslope invasion by Douglas-fir, which is not only more tolerant of shade, but also of drought. Therefore, assuming that evapotranspiration is increasing over the area, the Tavaputs Plateau may be experiencing a rapid upslope migration of drought-tolerant vegetation due to regional drying, with aspen's distribution suffering at the leading edge due both to drought itself as well as shading and further desiccation by the tolerant vegetation.

This climate–vegetation interaction may be exacerbated by ungulate densities exceeding their own long-term carrying capacities. Domestic ungulate densities increased from zero-value following European-American settlement, and Kay et al. (1999) found that elk densities over large parts of western North America are higher than at any other time in the archaeological record. Given a positive relationship between aspen predators and aspen predation, these increases in ungulate density over the Western U.S. may have hastened the aspen decline, but also may be a powerful tool in its restoration. Both of these relationships (as well as their interaction) are conjectural however, and time-serial maps of herbivore and conifer cover will be required to explore them.

4.4. Methodological implications

Wang (1990) argued that fuzzy landcover maps are preferable to their discretely valued counterparts due to fuzzy methods' retention of a greater proportion of the relevant information in remotely sensed, multispectral signals. Analogously, the only reason to employ habitone analyses in lieu of traditional, classification-based habitat analyses is to retain a greater proportion of the original, supposedly relevant information in the ecological response of the organism to its environment. The largest difficulty in using habitone maps and analyses is no longer computational; it is the inertia involved with changing our conception of landscapes from mosaics of discretely valued patches to gradients of more or less continuous variation.

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